

Genetic Characters of African Bees That Have High Adaptive Value in the Tropics

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Abstract.— The Ac gene present in Africanized *Apis mellifera* populations is male limited and confers bronze color to the abdomen; females are non-affected. The gene ac confers yellow abdomen equally to Italian female and male bees. African-mt-DNA is found in African and most Africanized populations, and European-mt-DNA occurs in European populations, and descendents. The original frequency in Camaquã in 1957 of ac was 0.939 and for Ac 0.061. In 1991, after about 68 generations, these frequencies changed to 0.038 to ac and 0.962 to Ac, what gives an adaptive value to ac in the tropics of 0.952 (considering 1.00 to Ac). The same may happen to the mt-DNAs, what may cause the mates European-mt-DNA queens X African-mt-DNA males to be less fit than the African-mt-DNA queens X European-mt-DNA males.

INTRODUCTION

There is a constant search in tropical research for characters that give to the bearer species a higher adaptive value when compared to European ones. This happened with corn, wheat, cabbage, apples, cattle, goats, etc. Many morphological, behavioral and physiological characters are being studied in European and African bees, and in their hybrids under different ecological conditions. Among them, two of the African characters are particularly interesting because within a few generations they became predominant in a tropical environment, but not in a temperate one. These characters are the gene Ac and the African-mt-DNA (that acts as a single gene). The population of this area is being well studied as far as their enzymes are concerned and show that the Africanized honeybee is an admixture of *Apis mellifera mellifera* (19.5%), *Apis mellifera ligustica* (3.8%) and *Apis mellifera scutellata* (76.7%) (Lobo et al. 1989; Del Lama et al. 1990).

The African-mt-DNA has been studied by Hall and Muralidharan (1989), Sheppard et al. (1991), Sheppard et al. (1991), Soares (1992) and others. It shows indications of high adaptive value in the tropics and low in southern South America (that has European-like climate), where it is dominated by European mt-DNA.

The Ac gene has been observed by Brazilian bee biologists since 1957. In 1969 the information published that it is male sex limited: it confers bronze color to the abdomen, especially to the tergites, while workers are yellow (Kerr 1969). It was present in 100% of the 145 queens collected in Africa and brought to Brazil in 1956. There was some information (Prof. V. Portugal Araujo, p.c.) that yellow males were occasionally present in Angolan populations. However, they were never seen by W. E. Kerr in his 1956 trip to Africa. It is an allele of b(=black) (Woyke and Kerr 1989), segregates 1Ac: 1ac in different genetic background, and is not linked to five components of aggressive behavior (Stort 1978).

MATERIAL AND METHODS

Between 19 July 1990 and 17 September 1991, 14 swarms of Africanized bees (*Apis mellifera* Linné) entered empty stingless bee hive boxes located in the Apiary of the Universidade Federal de Uberlândia, MG, Brazil. Hive boxes varied in size, from 15 to 45 litres in volume, located 420 km from Camaquã, the point of introduction of African bees, in 1957. All swarms contained many males. A sample of males was taken from each swarm and the numbers expressing the Ac and ac alleles were determined.

Males from an additional 17 colonies of Africanized bees were sampled from commercial honeybee hives that were occupied by Africanized swarms. Frequencies of the *ac* and *Ac* genes were calculated and compared with estimates of the frequencies of the same alleles in Camaquã in 1957.

RESULTS

Six hundred and ninety (690) *Ac* drones (0.9623) and 27 *ac* drones (0.0377) were sampled from the 31 colonies. No data for 1992 and 1993 were collected because all swarms (22 and 9, respectively) had only *Ac* drones. Drones in a swarm come from several colonies.

Some additional observations made are important to note: 1. Of the 14 swarms, only one had two queens (the same proportion found in Kerr et al. 1970), 2. in three swarms many bees with wax scales were seen, which indicates that bees of different ages were in the swarms, 3. in 1992 two and in 1993 two swarms arrived without males.

The lack of *ac* drones in 1992 and 1993 swarms is assumed to be a consequence of the population reaching fixation (100% *Ac* genes) or near fixation.

DISCUSSION

Since the gene *Ac* segregates independent of the *xo* gene, is independent of genes for defensive behavior and is an allele of **black** (*b*), the hypothesis that it was linked and continues to be linked with genes for high fitness after 68 generations of meiosis was discarded.

Several traits of Africanized bees have been and are being selected for Brazilian conditions (Page and Kerr 1991; Kerr 1992). The bees are becoming less aggressive; they are being selected for greater resistance to the *Varroa jacobsoni* mite (Moretto et al. 1991); they do not any more reject Italian foundation and they use fewer armadillo holes (Kerr 1992). The high frequencies of *Ac* and of African-mt-DNA are also a result of natural selection, since the degree of natural crosses between Africanized \times Italian and Italian \times Africanized are about equal when queens and drones of both races use the same mating ground

(Kerr and Bueno 1970).

In 1956, there were 400 Italian hives located in the same *Eucalyptus* forest into which 26 swarms of African bees escaped. All Italian colonies had *ac* and all African colonies had *Ac* genes. Therefore, assuming equal contributions of all escaped colonies to the breeding population, a frequency of 0.939 for the gene *ac* and 0.061 for *Ac* in 1957 was obtained for that original population. According to Winston (1992 pg. 40-42) an individual Africanized colony swarms about 16 times per year. Of course, this can only happen in the expansion phase of the population, before the population approaches the carrying capacity of the environment. According to Nascimento (1981 page 166), however, this figure, obtained in 1980, is 1.5 swarms per year. For our estimate a conservative "intermediate" figure of two successful swarms per colony per year will be used.

The original frequency F^{1957} of the gene *ac* (0.939) in 1957, multiplied, per generation, by its relative adaptive value (*w*) will give us the frequency F^{1991} for *ac* in 1991, that is 0.0377, 34 years later, or after 68 generations. Therefore: $F^{1991} = w^n \cdot F^{1957}$. In this formula *n*, the number of generations, is 68, F^{1957} is 0.939, F^{1991} is 0.0377 and our estimation for *w*, the fitness of *ac*, is 0.952 (considering 1.00 to *Ac*). This relatively low adaptive value *w* of *ac* is the reason for the almost universal presence of *Ac* in feral populations of *Apis mellifera* in tropical South America. It may be a similar reason for the the high frequency of African-mt-DNA found in Africanized populations, that is colonies of European-mt-DNA queens \times African-mt-DNA drones should be less fit than colonies of African-mt-DNA queens \times European-mt-DNA drones.

The bronze color of the *Ac* drones may not be the cause of its fitness, since the workers are yellow and heat preservation by dark color would be better in temperate climate; the physiological reason are being studied.

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Table 1. Data on swarms and hives at Uberlândia, Minas Gerais, Brazil, with reference to frequency of **Ac** and **ac** alleles.

Nº	Day	Arrival Hour	Hive Volume (Liters)	Frequency Of Genes	Place
01	19.07.90	15:00	27	25 Ac	Kerr's House
02	05.08.90	11:00	27	16 Ac	Kerr's House
03	12.08.90	08:45	(1)(3)	10 Ac	Kerr's House
04	19.08.90	10:45	27	16 Ac	Kerr's House
05	11.09.90	12:30	27	20 Ac	Kerr's House
06	21.07.91	13:15	27	24 Ac	Kerr's House
07	14.08.91	14:20	27	15 Ac	Kerr's House
08	04.08.91	15:15	27	08 Ac	Kerr's House
09	05.08.91	14:28	(1)	05 Ac	Kerr's House
10	08.08.91	15:00	27	10 Ac	Kerr's House
11	09.08.91	12:00	45	23 Ac	Kerr's House
12	14.08.91	14:20	27 (3)	14 Ac	Kerr's House
13	27.08.91	12:29	27	47 Ac	Kerr's House
14	24.11.91	(1)	15 (3)	34 Ac	Kerr's House
15	12.05.91	(2)	—	43 Ac	Alvorada Farm
16	11.08.91	(2)	—	23 Ac	Rio Pedras Farm
17	11.08.91	(2)	—	23 Ac	Rio Pedras Farm
18	11.08.91	(2)	—	23 Ac	Rio Pedras Farm
19	11.08.91	(2)	—	23 Ac	Alvorada Farm
20	11.08.91	(2)	—	23 Ac	Alvorada Farm
21	11.08.91	(2)	—	23 Ac	St ^a . Rita Farm
22	06.08.91	(2)	—	24 Ac	St ^a . Rita Farm
23	06.08.91	(2)	—	24 Ac	St ^a . Rita Farm
24	04.09.91	(2)	—	24 Ac	Alvorada Farm
25	04.09.91	(2)	—	23 Ac	Alvorada Farm
26	04.09.91	(2)	—	24 Ac	Rio Pedras Farm
27	06.08.91	(2)	—	24 Ac	Rio Pedras Farm
28	17.09.91	(2)	—	24 Ac	Alvorada Farm
29	17.09.91	(2)	—	23 Ac	Alvorada Farm
30	17.09.91	(2)	—	23 Ac	Alvorada Farm
31	17.09.91	(2)	—	34 Ac	Rio Pedras Farm

690 Ac (96.23%)

27 ac (3.77%)

(1) Hour not noticed.

(2) Langstroth hive.

(3) Enormous swarm.